

THE POSTCRANIAL SKELETON OF *ROBERTIA BROOMIANA*, AN
EARLY DICYNODONT (REPTILIA, THERAPSIDA) FROM THE SOUTH
AFRICAN KAROO

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(With 15 figures)

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ABSTRACT

The postcranial skeleton is described. Some comparison with later dicynodonts is made.

Where possible the muscles of the pectoral and pelvic girdles are reconstructed. The forelimb took up a sprawling position relative to the body. The biceps, brachialis, coracobrachialis and pectoralis muscles were all well developed as adductors. Limb extension by the powerful triceps was probably an important contribution to the otherwise short stride. The supracoracoideus probably inserted on the medial side of the scapula, passing beneath the everted acromion process. It is argued that development of the acromion process might have been in relation to the use of the clavicle as a movable rod, rather than an inflexible brace, in the girdle.

The femur took up a sprawling position in the body. The main retractor muscle was the iliofemoralis. The position of the head of the femur on the anteromedial extremity of the bone is seen as an adaptation for lengthening the stride of the hind limb. The ilium is not produced far anteriorly as in later dicynodonts, and the trochanter major is not well developed. It is postulated that in later dicynodonts the further development of the trochanter major and the iliofemoralis was to produce long axis rotation in the stride.

In the vertebral column flexibility in a lateral plane was provided for by the flattened zygapophyses.

It is suggested that *Robertia* was a lizard-like animal, possibly partly insectivorous.

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INTRODUCTION

The dicynodonts, a group of herbivorous mammal-like reptiles, probably arose at some time in the Lower Permian. After a period of considerable success in terms of both species number and diversity, most forms became extinct at the

end of the Permian. Only one major lineage survived into the Triassic, undergoing a small adaptive radiation.

The earliest member of the Dicynodontia (*sensu* Romer 1966) is *Eodicynodon oosthuizeni* (Barry 1974), reputedly from Ecca beds of South Africa. These beds lie at the base of the fossil-bearing Beaufort Series of the South African Karoo sediments, and are generally considered to be non-fossiliferous. Before the discovery of *Eodicynodon* the earliest dicynodonts were known from the lowermost zone of the Beaufort Series, the *Tapinocephalus* Zone. There is some dispute over the exact age of *Eodicynodon* (A. W. Keyser 1978 pers. comm.), but it seems that even if it is actually a *Tapinocephalus* Zone form, it is from a lower level in that zone than any other fossil.

Eodicynodon retains several primitive features relative to other dicynodonts: the secondary palate is short, the premaxillae are paired, the vomers are paired, there is a lateral pterygoid flange. No postcranial remains have been recovered.

Several genera of dicynodonts have been described from the higher levels of the *Tapinocephalus* Zone in South Africa. Even at this early stage the dicynodonts had diversified, although remaining small and being characterized by the possession of postcanine teeth. It is likely that of the nine or so genera described in the literature as *Tapinocephalus* Zone forms, probably about five are actually valid. Work in progress by Cluver & King attempts to establish these groups. One of the groups is founded on *Robertia broomiana* (Boonstra 1948; Toerien 1953) and contains *Tapinocephalus* Zone forms having a few small postcanine teeth, a notched palatal rim with a maxillary blade posterior to the notch and a lateral dentary shelf which tends to occlude the intra-mandibular fossa. This group contains the only specimens of *Tapinocephalus* Zone postcranial material which can be assigned to a genus and species, being found in association with cranial material.

The material in question (SAM-11885) is that referred to by Boonstra (1966) as 'Endothiodontid. A number of fairly complete skeletons. Michau's Request, Beaufort West. Low *Tapinocephalus* Zone.' Femur, lower forelimb and lower hind limb are figured. The skulls included in SAM-11885 have the following features in common with the type of *Robertia broomiana*: postcanine teeth (Fig. 1:t), the maxillary notch (Fig. 1:n), the lateral dentary shelf (Fig. 1:d s), and reduced palatines (Fig. 1:pal). (In all figures a broken line indicates the reconstruction of a damaged area, unless otherwise specified.) They are here assigned to that genus and species.

A complete description and detailed discussion of the postcranial skeleton of *Robertia* is warranted since it represents the earliest dicynodont postcranial material known. Previous descriptions of postcranial skeleton (excluding Boonstra 1966) have been concerned with later fossils, for example *Kingoria* (Cox 1959), *Cistecephalus* (Cluver 1978), *Kawingasaurus* (Cox 1972), *Dicynodon trigonocephalus* (King 1981), *Tetragonias* (Cruickshank 1967), *Kannemeyeria* (Pearson 1924) and *Placerias* (Camp & Welles 1956). Various aspects of the

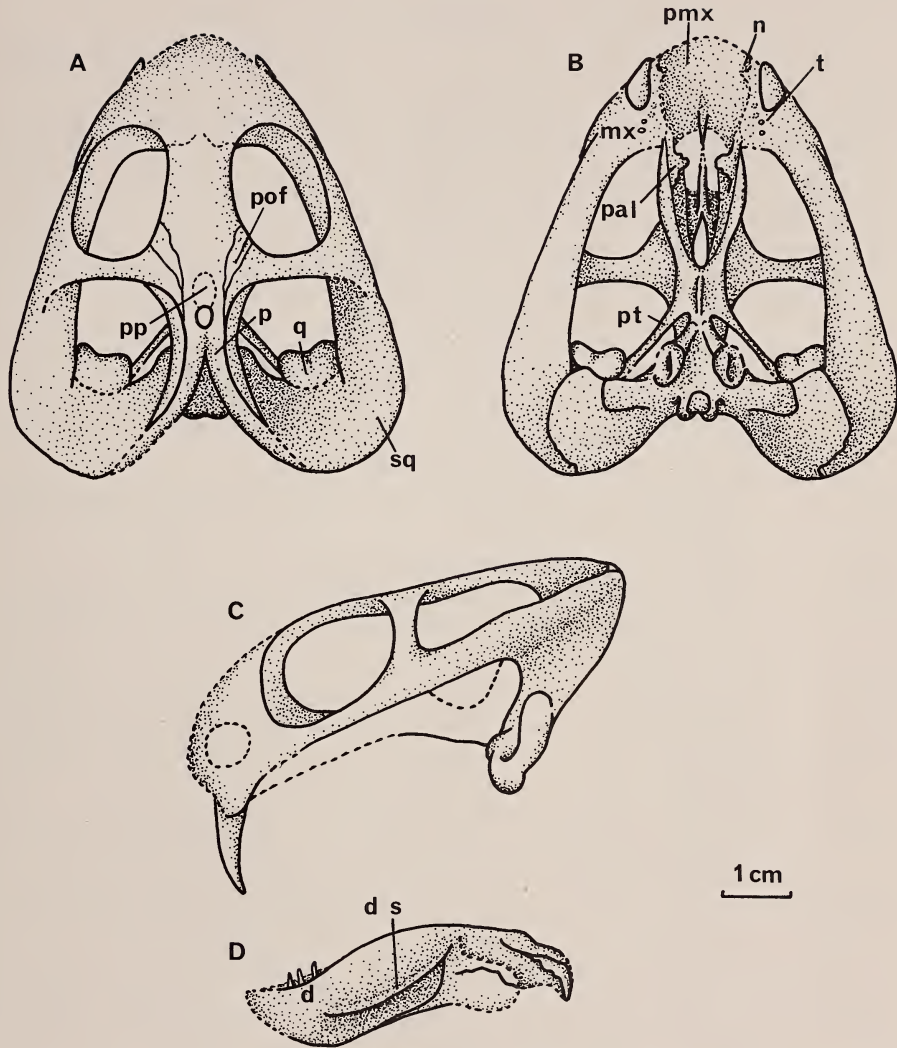


Fig. 1. *Robertia broomiana*, skull and lower jaw. A. Skull dorsal. B. Skull palatal. C. Skull lateral. D. Lower jaw lateral. (Reconstructed from casts 1 and 2.) (For abbreviations see p. 229.)

skeleton of such dicynodonts are extremely specialized when compared to other therapsids (see also Parrington 1955) and it is hoped that study of an early form may shed light on the processes and pathways which brought about these specializations. Information on their postcranial anatomy may also help in the interpretation of the kinds of habitats which these early forms occupied and indicate why the dicynodonts did not apparently radiate explosively until later on in the *Cistecephalus* Zone.

MATERIAL

The material consists of twelve latex casts in the South African Museum, Cape Town (SAM-11885). The original bones had been dissolved out of the intractable matrix by using a strong acid, so that the resulting casts are positive impressions. The preservation of the bones was in parts excellent, and the casts represent the bone detail very well. At least three partial skeletons were present in several blocks of matrix. There is very little variation between the skeletons, making it entirely reasonable that they represent one species. There are several runs of articulated vertebrae, and several associated girdles with limb bones. The distribution of skeletal elements in the various casts is as follows:

- Cast 1. Partial skull and lower jaw. Radius, ulna and manus.
- Cast 2. Skull and lower jaw in palatal view. Neck vertebrae.
- Cast 3. Lower jaw. Scapula, humerus, radius and ulna, carpals. Dorsal aspect of a sequence of vertebrae. Ribs.
- Cast 4. Humerus, interclavicle, partial clavicles.
- Cast 5. Two scapulae, partial coracoid and precoracoid. Humerus. Disarticulated vertebrae and ribs.
- Cast 6. Sequence of mid-dorsal ribs and vertebrae.
- Cast 7. Femur (1), fibula, incomplete pes. Tail vertebrae, right and left ilium and pubo-ischiadic plate, two incomplete sacral vertebrae. Femur (2).
- Cast 8. Proximal end of femur and dorsal edge of ilium which are counterparts of femur (2) and left ilium of cast 7. Run of vertebrae and ribs.
- Cast 9. Femur, pes, fibula and tail vertebrae which are counterparts of femur (1), fibula, pes and tail vertebrae of cast 7.
- Cast 10. Clavicle, a sequence of vertebrae and some ribs. Distal end of a humerus; radius and ulna, carpals.
- Cast 11. Humerus, radius and ulna, carpals which are counterparts of cast 10.
- Cast 12. Disarticulated ribs. Partial scapula and coracoid. Sternum. Humerus (3) and radius and ulna. Humerus (4) in dorsal view.

Two other dicynodonts have been used for comparative purposes. One is a medium-sized *Daptocephalus* Zone (*sensu* Kitching 1977) dicynodont, *Dicynodon trigonocephalus* (King 1981) which has a virtually complete postcranial skeleton. The other (TSK 83, a specimen from T. S. Kemp's collection housed in the Oxford University Museum) is a collection of several partly-disarticulated small skeletons from the *Daptocephalus* zone of Zambia (Madumabisa Mudstones horizon). These conform to Cluver & Hotton's (1981) definition of *Dicynodon*, having a dorsal dentary sulcus, no lateral dentary shelf, an unnotched maxillary rim, and dentary tables. The specimens may be immature individuals, being small, having unerupted tusks, and open sutures.

In the following description and analysis the positions of the origins and insertions of muscles have been reconstructed with reference to Romer (1922). The possibilities of movement of the limbs were investigated by manipulating plasticine models of the bones.

DESCRIPTION AND FUNCTIONAL ANATOMY

FORELIMB AND PECTORAL GIRDLE

Four well-preserved scapulae are present (Fig. 2). The dorsal blade is rather narrow. It curves medially and its lateral surface is concave anteroposteriorly. The anterior edge is thick and drawn up into a prominent ridge facing laterally (Fig. 2: r). The ridge continues ventrally into the acromion process (Fig. 2: ac p) which is large and strongly everted. The medial side of the acromion process and the body of the scapula adjoining it are hollowed out into a shallow fossa (Fig. 2: s fo). The anterior edge of the scapula just below the acromion process is smooth and this, together with the eversion of the process, would allow the supracoracoideus muscle to pass on to the medial side of the scapula and attach into the shallow fossa there. The medial surface of the scapula is strongly convex anteroposteriorly and drawn up into a ridge at the height of the convexity (Fig. 2: m r). This may mark the division between the origins of the supracoracoideus and subscapularis muscles. Since the ventral part of the scapula blade is so slender, neither of these muscles could have had an extensive origin here.

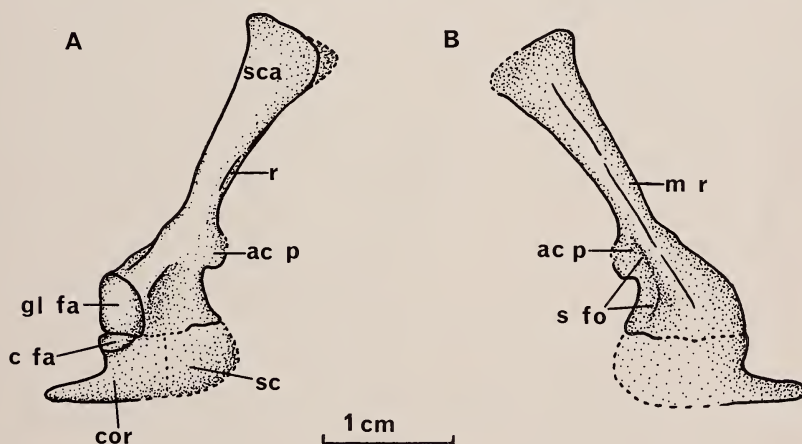


Fig. 2. *Robertia broomiana*, shoulder girdle. A. Lateral. B. Medial. (Reconstructed from casts 5 and 12.)

Below the acromion process the scapula fans out to form the articulation with the coracoid, and the glenoid. The scapula glenoid facet (Fig. 2: gl fa) is approximately circular. It faces downward, backward and slightly outward if the blade of the scapula is tilted slightly forward (Fig. 2). The facet is shallowly concave dorsoventrally and convex anteroposteriorly. The coracoid is well preserved only in medial view but the glenoid facet (Fig. 2: c fa) appears to face backward and upward. The precoracoid appears to be of the usual dicynodont conformation but it is badly preserved and the precoracoid foramen is not evident.

Much of the interclavicle (Fig. 3b) is preserved. It is a rectangular sheet of bone drawn up into a low boss in the midline of the ventral surface (Fig. 3B: b). On either side of the boss the surface may be hollowed out into a very shallow and indistinct fossa, presumably for the attachment of the pectoralis muscles. In one specimen the proximal ends of the clavicles are preserved *in situ* on the interclavicle (see Fig. 3B). The proximal end of the clavicle is flattened and spoon-shaped, bearing a distinct ridge (Fig. 3B: r) which continues on to the

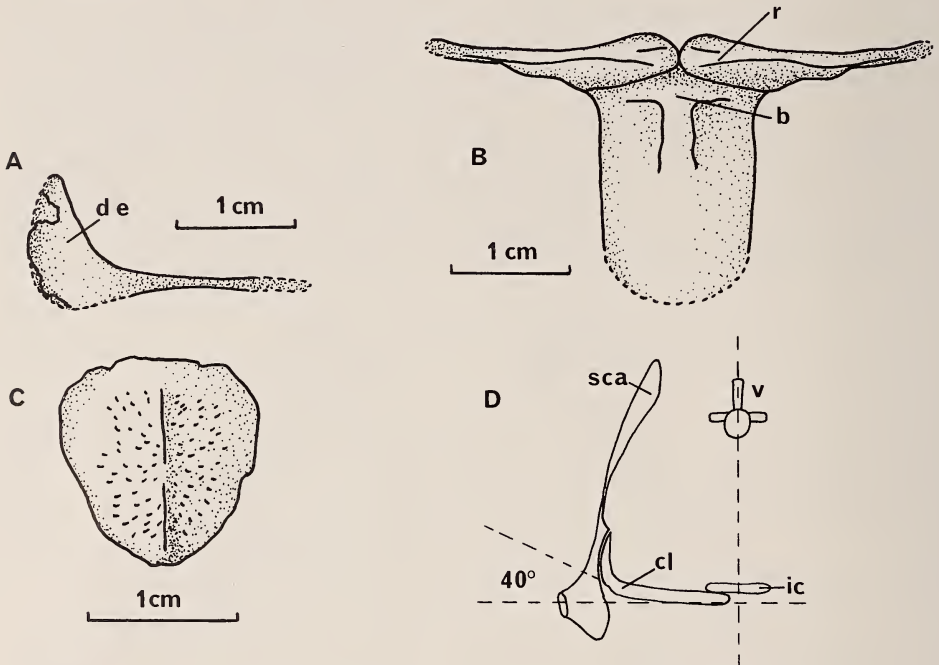


Fig. 3. *Robertia broomiana*, clavicle, interclavicle and sternum. A. Clavicle anterior. B. Clavicles and interclavicle ventral. C. Sternum ventral. D. Diagram to show the relative orientations of the elements of the girdle (explained further in the text), anterior. (Reconstructed from casts 4, 10, and 12).

shaft of the bone. The distal end is also expanded, in a direction at right angles to the expansion of the proximal end. The distal end is approximately triangular (Fig. 3A: d e), very extensive and rather robust.

Much of the sternum is present, though poorly preserved (Fig. 3C). It would seem to take the form of an oval plate which tapers slightly towards its posterior end. It bears a slight median ridge. The bone surface is uneven in texture, bearing irregular striations. The posterior and anterior edges are somewhat thickened. Other edges are not sufficiently well preserved to determine thickness, or whether rib articulations were present.

The humerus (Fig. 4) is well preserved. The distal and proximal ends of the bone are expanded in typical dicynodont fashion. The head (Fig. 4: hd) faces

medially and somewhat dorsally but is not pronounced. Anterior to the head the bone is drawn into the deltopectoral crest (Fig. 4: d p c). Presumably the deltoideus muscle inserted mainly on the dorsal surface of the crest, while the pectoralis muscles inserted on the rugose ventral surface (Fig. 4: v s). On the dorsal surface the crest is marked off abruptly from the shaft of the bone by a pronounced ridge (Fig. 4C: r) posterior to which is a triangular fossa (Fig. 4C: t fo). The dorsal surface is, therefore, quite unlike that of *Dicynodon trigonocephalus* (Fig. 4D) where there is no such fossa in the middle of the bone. Instead, in *D. trigonocephalus* there are a shallow fossa on the posterior margin of the bone and a strong tubercle (Fig. 4D: tub) which have been interpreted as

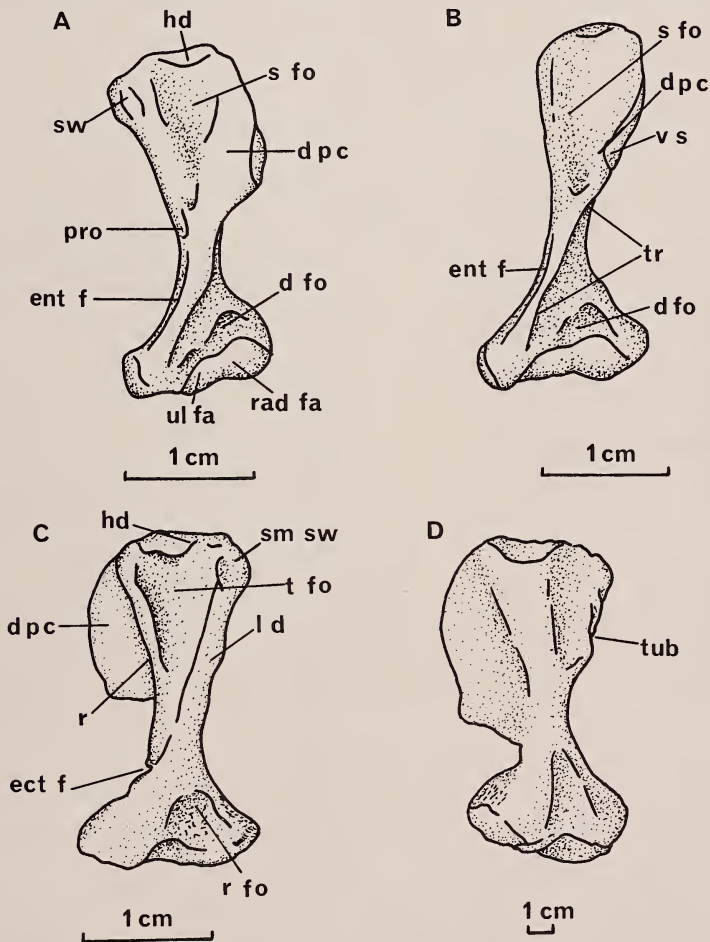


Fig. 4. *Robertia broomiana*, left humerus. A. Proximal ventral. B. Distal ventral. C. Proximal dorsal. D. Humerus of *Dicynodon trigonocephalus* in proximal dorsal view. (A reconstructed from cast 4; B reconstructed from cast 5; C reconstructed from cast 12, humerus 4.)

the attachment site of the triceps (King 1981). No tubercle is present on the humerus of *Robertia* and the attachment of the triceps humeralis lateralis is here taken to be in the extensive triangular fossa. Two small swellings are found on the posterior edge of the bone, one near the head of the bone which encroaches on the dorsal surface (Fig. 4C: sm sw), and the other more distal (Fig. 4C: l d). These may represent the insertions of the subscapularis and latissimus dorsi, respectively.

The ventral surface of the proximal end is excavated into a shallow but extensive fossa (Fig. 4A–B: s fo) between the deltopectoral crest and the posterior margin. This probably represents the insertion of the coracobrachialis muscle. Posterior and distal to this fossa is a marked protuberance (Fig. 4A: pro) possibly indicating the coracobrachialis longus insertion. The posteromedial corner of the posterior margin of the ventral surface is also rather swollen and striated (Fig 4A: sw). This may mark the encroachment on the ventral surface of the insertion of the subscapularis muscle.

The distal ventral surface bears an entepicondylar foramen (Fig. 4A–B: ent f). In addition, several humeri also show evidence of the ectepicondylar foramen (Fig. 4C: ect f). In dorsal view a notch leading from the anterodorsal surface to the ventral surface can be seen. The notch is continued either side by a groove running from the dorsal surface in a ventral, anterior, and distal direction.

The facets for articulation of the radius and ulna (Fig. 4A: rad fa. ul fa) are largely ventral. Anterior to these facets is a deep and well-defined fossa (Fig. 4A–B: d fo). This may indicate the site of insertion of ligamentous connections to the lower limb.

The position of the brachialis inferior is shown quite clearly on several specimens, being delimited by the pronounced dorsal ridge which separates the triceps lateralis fossa from the deltopectoral crest. The brachialis origin presumably starts on the ventral distal surface anterior to the entepicondylar foramen. It passes proximally and dorsally on to the body of the deltopectoral crest to lie posterior to the deltoideus insertion. The whole of the area of origin described forms a smooth and continuous trough (Fig. 4B: tr).

On the dorsal surface a fossa (Fig. 4C: r fo) is present near the posterior margin of the bone. The surface of the fossa is rough and the posterior and distal edges of the bone are deeply striated. This would be a reasonable position for the origin of the triceps humeralis medialis.

The radius and the ulna are shown in Figure 5. In the following description it is assumed that the bones are oriented at right angles to the humerus. Each is a slender element approximately three-quarters the length of the humerus. The ulna bears a weak olecranon process (Fig. 5B–C: o p). The anterior surface of this bone is excavated into an extensive fossa proximally (Fig. 5B: pr fo). The medial edge of this is continued ventrally as a pronounced ridge (Fig. 5B: r) forming the medial edge of the bone over most of its length, but turning on to the anterior surface far ventrally. The proximal fossa extending down from the olecranon process was presumably for the triceps insertion, while the long ridge

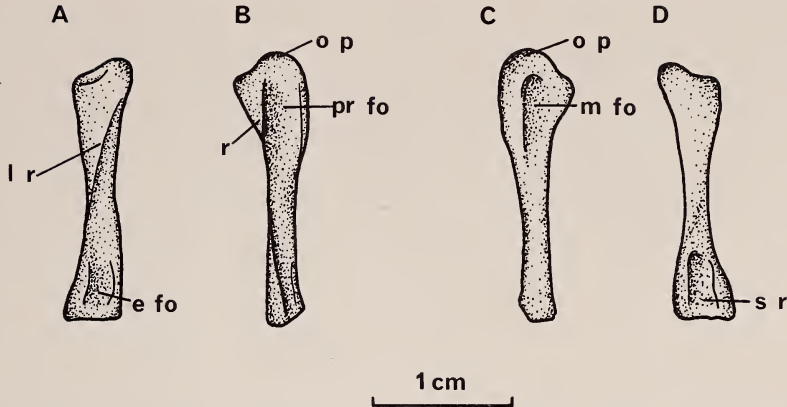


Fig. 5. *Robertia broomiana*, right radius and ulna. A. Radius anterior. B. Ulna anterior. C. Ulna posterior. D. Radius posterior. (Reconstructed from cast 3.)

probably took the biceps insertion. The posterior surface of the ulna also bears a marked excavation proximally (Fig. 5C: m fo), possibly the insertion of an ulnar flexor from the entepicondyle.

The distal end of the ulna is approximately oval, concave anteroposteriorly and convex mediolaterally. The distal end of the radius is greater in area and flatter.

The radius itself bears a distinct elongate fossa (Fig. 5A: e fo) on its anterior distal surface. A low ridge runs along the anterior surface from the proximal lateral to the distal medial corner (Fig. 5A: l r). This probably was the site of insertion of the brachialis inferior. A much shorter ridge runs along the posterior surface of the distal end (Fig. 5D: s r).

The forefoot is well represented but not complete. Figure 6 shows a reconstruction based on all the specimens preserved. Of the carpus an ulnare, a radiale and an intermedium can be identified. A small bone near to the radius of one specimen may represent a pisiform. The best-preserved carpus shows three more distinct bones, two of which are probably centralia, but it is difficult to be certain. One of the elements (Fig. 6: ce?) is rather large and may indicate fusion of two centralia.

Metacarpals I to V are present. They are elongate bones, very slightly flattened dorsoventrally. Number I is significantly smaller than the others. No complete digit V is present but all others are, and the phalangeal formula is 2-3-3-3-(?). No reduced or fused phalanges are apparent. Each terminal phalanx is a blunt claw, displaying a pronounced boss on its plantar surface (Fig. 6B: b). The phalanges in each digit increase in size proximally. The phalanges of digit III are the longest, indicating that the hand might have been approaching a symmetrical condition.

The hand gives the impression of being long-fingered and flexible. In one specimen the metacarpal and phalanges of the longest finger together are as long

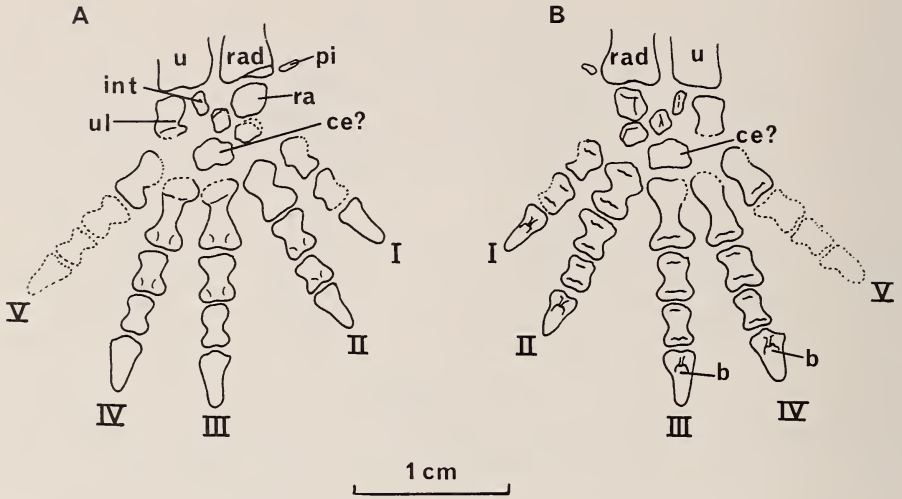


Fig. 6. *Robertia broomiana*, right forefoot. A. Dorsal. B. Plantar. (Reconstructed from casts 1, 3, and 11.)

as the radius. Such a large hand might have acted simply as a platform to support and stabilize the body, but, although long, the hand is not particularly broad. The stout claws may rather suggest a tearing or scratching function.

Discussion

The above morphological and anatomical considerations, when subjected to a functional analysis, indicate that the forelimb took up a primitive sprawling position relative to the body, and that, on the whole, the muscle pattern of the forelimb and girdle was conservative. However, many of the specialized features of later dicynodonts are already present in the *Tapinocephalus* Zone form.

The orientation of the glenoid depends on how the scapula is oriented in the body. This is difficult to deduce in a disarticulated skeleton, but one clue is the position and direction of the clavicle and interclavicle. The shaft of the clavicle leaves the interclavicle in the midline, either horizontally or at a very small angle (Fig. 3D). The distal part of the clavicle then turns backward (about 40°) while expanding dorsally. The posterodistal edge of the bone is a smooth arc congruent with the arc of the scapula anterior edge above the acromion process. Because of the orientation just described, the clavicle arc is positioned sloping slightly forward in the body and therefore the scapula edge must do the same. The overall orientation of the scapula is, therefore, with the blade sloping forward at an angle of approximately 60° to the horizontal, and curving dorso-medially. The glenoid facet will then face mostly laterally and also posteriorly. When the humerus is articulated in the glenoid it takes up a sprawling position. An erect or semi-erect position is not possible because the head of the bone is mainly dorsal and in the middle of the proximal end. In the sprawling

position a rather limited protraction–retraction arc is possible before the head is disarticulated or before the deltopectoral crest touches the girdle. For the latter reason, also little long axis rotation is possible. Elevation and adduction of the distal end of the bone does seem to be possible.

The facets on the humerus for articulation with the radius and ulna are almost completely ventral, indicating that the antebrachium was positioned at right angles to the humerus as would be expected in a sprawling-gaited animal.

With the forelimb so positioned, there is a tendency for the animal's body to collapse through the girdle under the action of gravity unless strong postural muscles are present. Such muscles can prevent collapse only if the angle between the two elements that are collapsing is increasing, as then shortening of a muscle can restore the former relationship of the two elements. Therefore, in a sprawling-gaited animal the postural muscles important in preventing collapse are the ventral adducting muscles, the biceps, brachialis, coracobrachialis and pectoralis. The sites of attachment in *Robertia* show that these muscles were all very well developed (Fig. 7A, C–E). The triceps does not have this kind of postural function, neither do the dorsal muscles such as the deltoideus, supracoracoideus or subscapularis. The supracoracoideus would have protracted the limb, the deltoideus elevating it. The latissimus dorsi presumably played a part in retracting the limb, helped by the subscapularis. This last muscle might have caused some long axis rotation if its insertion had spread to the ventral or even posterior surface of the scapula. A small amount of rotation is permitted by the joint and would have the effect of forcing the antebrachium backward. This is important since the powerful triceps muscle could then extend the limb forcing the body forwards. This could have been an important contribution to the otherwise short stride.

The eversion of the acromion process and medial origin of the supracoracoideus are specializations of dicynodonts unknown in the other non-cynodont mammal-like reptiles. As seen, they are already present even in primitive dicynodonts. The advantage of such an arrangement is not immediately obvious. In other reptiles the supracoracoideus and scapulohumeralis attach to the precoracoid and anteroventral part of the scapula. The latter is much more extensive anteroposteriorly than in dicynodonts, and therefore ensures an adequate fibre length of the supracoracoideus. In moving the origin of the muscle on to the medial side of the scapula in dicynodonts, the length of the muscle is not greatly increased since the part of the scapula anterior to the glenoid has been reduced in length. Neither is the direction of the movement produced by the muscle significantly different. The prime selective pressure for development and eversion of the acromion process was probably not then to produce a supracoracoideus which was longer or acted in a different direction. Indeed, there must have been a time immediately before the muscle passed on to the medial side when the anterior part of the scapula had been cut back, producing the incipient acromion process and actually reducing both the area and fibre length of the supracoracoideus.

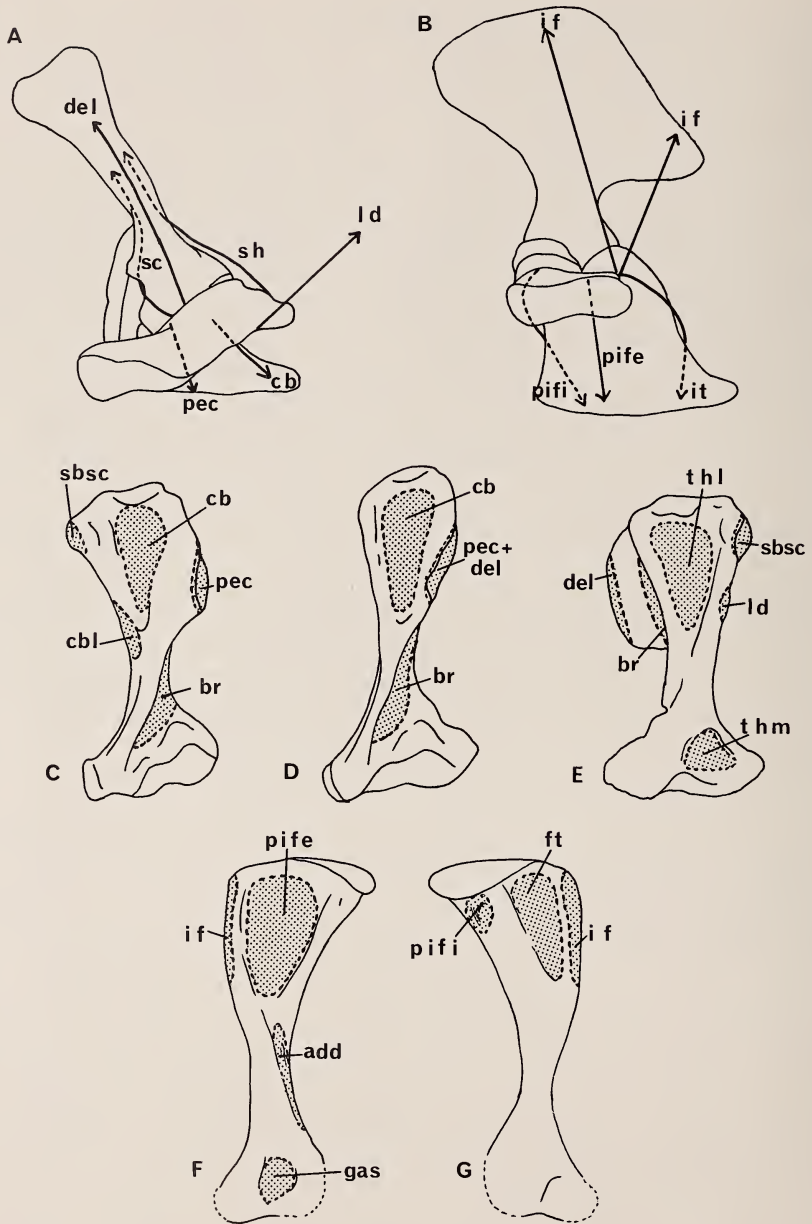


Fig. 7. *Robertia broomiana*, a reconstruction of the pelvic and pectoral musculature. A. The approximate postulated lines of the muscles of the pectoral girdle. B. The approximate postulated lines of the muscles of the pelvic girdle. C-E. Insertions of muscles on the humerus. F-G. Insertions of the muscles on the femur. (In A-B a broken line indicates muscle behind a bone; in C-G a broken outline and stippling indicates the approximate insertional area.)

The acromion process might instead have developed to provide a firmer attachment for the clavicle. However, in the dicynodont shoulder girdle there is less contact between the acromion and the clavicle compared to the pelycosaur condition. Instead the clavicle may be tending to act more as a rod about which the interclavicle and scapula may pivot, rather than a static brace for the girdle. This would seem likely since intra-girdle movements causing rotation of the glenoid may occur in *Dicynodon trigonocephalus* (King 1981). Also, the transition from the pelycosaur screw-shaped glenoid producing a rigidly-defined movement pattern of the humerus (Jenkins 1971) to the open notch-shaped glenoid in therapsids may indicate increased flexibility of the limb. This may be associated with the need for prey capture or traversing uneven terrain or even social behaviour. A less rigid girdle would facilitate such movements as well as possibly increase the stride by allowing a longer excursion of the humerus (King 1981).

In order for the clavicle to act as a rod connecting the interclavicle and scapula, its contacts with them must be reduced to pivoting points. This would initially involve reduction of the anteroventral area of the scapula, leaving the clavicle contact (acromion process) standing proud. At this stage the origin of the supracoracoideus would be diminishing since it cannot extend over the lateral surface of the scapula which is occupied by the deltoideus, and it cannot yet reach the medial surface. At this stage perhaps its role was augmented by the deltoideus and latissimus dorsi. If the acromion process were now everted, for example to increase the length of the clavicle, the supracoracoideus would gain access to the medial side of the scapula, and relieved of the supracoracoideus origin, the anteroventral part of the scapula could be reduced further. It is possible, though, that the supracoracoideus did not play an over-important part in limb movement again, since the latissimus dorsi is probably a more powerful retractor and the deltoideus a better elevator.

HIND LIMB AND PELVIC GIRDLE

The femur (Fig. 8A–B) is a gently S-shaped bone with a distinct shaft. The head is on the anterior margin of the proximal end and is more extensive on the dorsal surface. There is no neck separating the head from the rest of the bone. Ventrally (assuming the femur to be in a position at right angles to the acetabulum) the bone bears a large triangular fossa on its proximal half (Fig. 8A: t fo) which is presumably the insertion of the pubo-ischio-femoralis externus muscle. The anterior boundary of this fossa is a low ridge (Fig. 8A: l r) which bears a rugose striated area just distal to the head (Fig. 8A: r a). This may possibly represent the remains of the internal trochanter seen in pelycosaurs and other therapsids but otherwise absent from dicynodonts. The posterior boundary of the triangular fossa is not as pronounced as the anterior, but a flat ridge (Fig. 8A: f r) is developed which continues on to the shaft of the bone in an anterolateral direction, probably marking the insertion of the ventral adductor muscles. The ridge terminates just proximal to a deep, oval fossa (Fig. 8A: o fo)

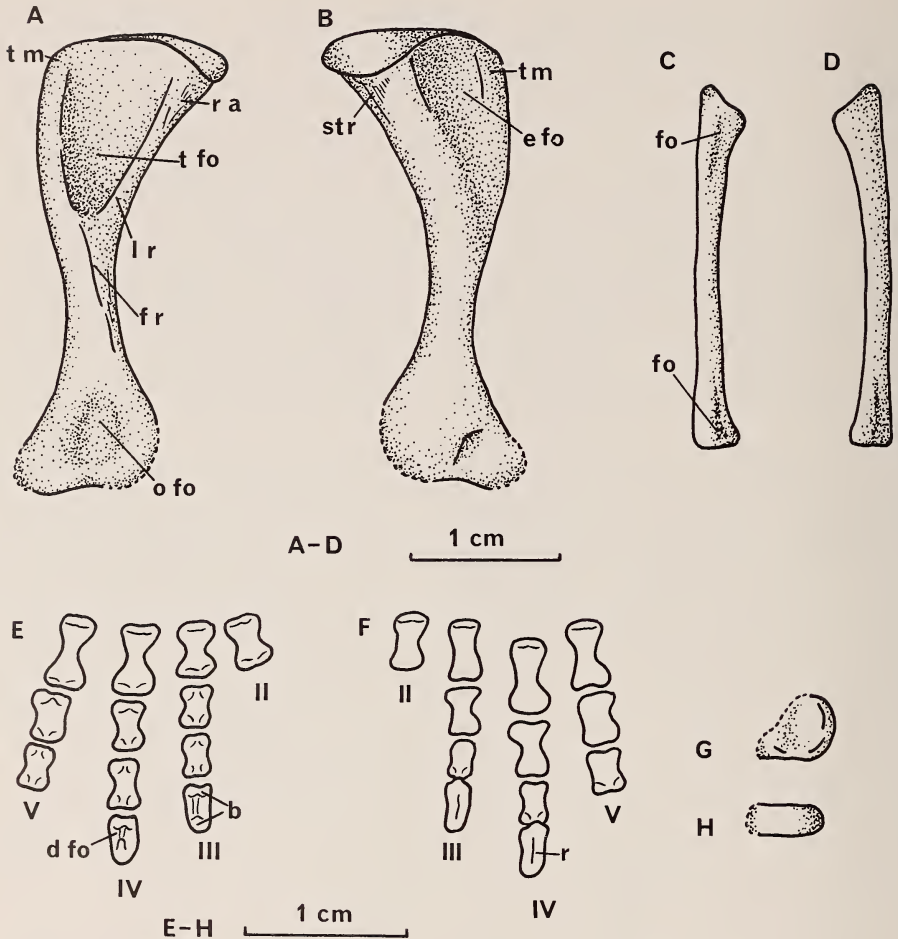


Fig. 8. *Robertia broomiana*, left femur, fibula and hind foot. A. Femur ventral. B. Femur dorsal. C. Fibula posterior. D. Fibula anterior. E. Pes plantar. F. Pes dorsal. G. Tarsal(?) dorsal. H. Tarsal(?) posterior. (Reconstructed from casts 7 and 9.)

occupying the distal part of the ventral surface, indicating the attachment of the gastrocnemius muscle. The trochanter major (Fig. 8A-B: tm) is not at all prominent and is not cut off sharply from the shaft of the bone distally as is the case in *Dicynodon trigonocephalus*. No fourth trochanter is visible.

The dorsal surface of the bone bears a prominent patch of striations (Fig. 8B: str) on its anterior margin just distal to the head. This is a likely insertion for the pubo-ischio-femoralis internus muscle. Posterior, to this area the femur is excavated into an elongate fossa which extends well down the bone towards the constricted middle portion (Fig. 8B: efo). This is probably the extensive origin of the femorotibialis muscle. Posterior to this fossa the edge of the bone is thickened and striated as it is on the ventral surface. Presumably the iliofemor-

alis muscle inserted here, mainly dorsally but also conceivably posteriorly and ventrally.

Only one hind limb epipodial is present. It is identified as the left fibula (Fig. 8C–D). It is a slender bone approximately three-quarters of the length of the femur. The bone is almost straight, the medial edge being only slightly concave. The posterior surface bears two shallow fossae, one in the proximal and the other in the distal half of the bone (Fig. 8C: fo).

Of the pes digits III and IV are complete, V and II are incomplete and I is missing (Fig. 8E–F). Metatarsals II to V are present. One element only of the tarsus is preserved, a small disc-shaped bone (Fig. 8G–H). As in the hand, the metatarsals decrease in size from digit V to digit II. The phalanges decrease in size within a digit distally. The terminal phalanx is a claw, more rounded than that of the hand and bearing a distinct ridge dorsally (Fig. 8E: r). Ventrally the claw bears a boss (Fig. 8F: b) near both its anterior and posterior margins. The area in between is excavated into two small deep fossae (Fig. 8F: d fo).

Most of the ilium is preserved. It is a fan-shaped plate of bone as in most dicynodonts but is expanded anteriorly only to a small degree (Fig. 9). On the anterior margin of the lateral surface it is possible that there is a slight hollowing-out of the bone surface (Fig. 9B: h) distinct from that occupying most of the rest of the lateral surface (Fig. 9B: la fo). The anterior excavation may represent the origin of the iliotibialis muscle, while much of the rest of the bone surface would be occupied by the origin of the iliofemoralis muscle.

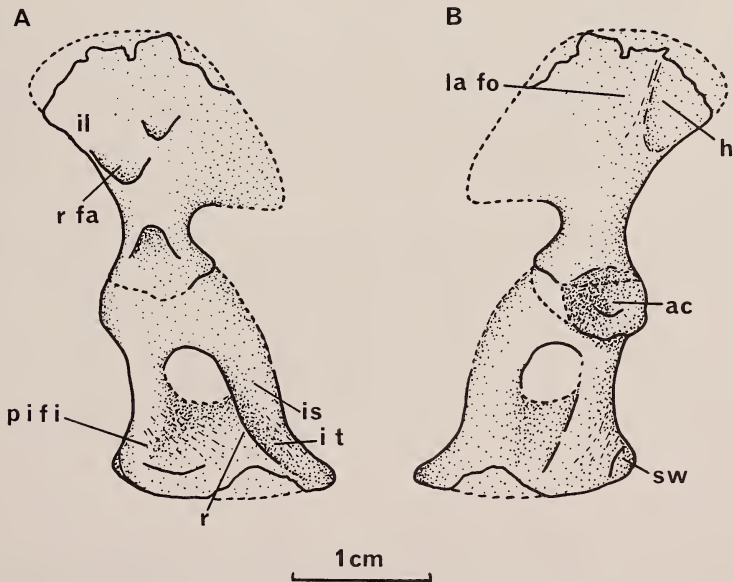


Fig. 9. *Robertia broomiana*, right ilium and pubo-ischiadic plate. A. Medial. B. Lateral. (Reconstructed from casts 7, 8, and 9.)

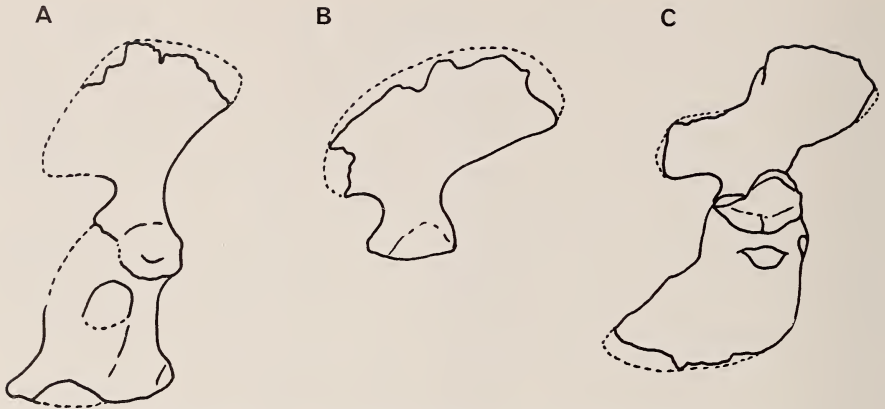


Fig. 10. A comparison of the pelvic girdles of some dicynodonts. A. *Robertia broomiana*. B. T. S. Kemp Collection, Oxford University Museum 83. C. *Dicynodon trigonocephalus*. (B and C reduced to the same width across the ilium-pubo-ischiadic plate symphysis as A.)

The posterior part of the ilium of this specimen is more damaged, but this region of the bone does appear to be quite well developed (Fig. 10).

The medial surface of the ilium shows one clear sacral rib facet (Fig. 9A: r fa). Others are indistinct.

The fused pubis and ischium form a flattish square plate, drawn out into a stout process at its posteroventral corner. The anterior margin is thickened and bears a small swelling (Fig. 9B: sw) ventrally which constitutes the pubic tubercle. More dorsally, the ischiadic contribution to the acetabulum is found. The acetabulum tends to be occluded by the dorsal margin (formed by the ilium) which faces somewhat ventrolaterally. The ventral margin of the acetabulum faces dorsolaterally. The ilium and pubo-ischiadic plate appear to contribute equally to the acetabulum which is situated on the anterior margin of the girdle (Fig. 9B: ac).

A fairly large obturator foramen occupies the middle of the pubo-ischiadic plate. On the medial surface the posterior edge of the foramen is drawn up into a sharp ridge (Fig. 9A: r). Posterior to this ridge is a rugose area, probably the site of the origin of the ischiotrochantericus (Fig. 9A: i-t). Anterior and ventral to the obturator foramen the ventral surface bears a distinct area of striations aligned anterodorsally. This patch of striations does not reach the ventral edge of the plate. It presumably marks the origin of the pubo-ischio-femoralis internus (Fig. 9A: p i f i).

Discussion

As far as can be determined, the femur took up a sprawling position in the acetabulum. The head of the femur is pronounced dorsally and not set off from the rest of the bone at all, and in an erect or even semi-erect position would not contact the articular surface. A very substantial building up of the head in

cartilage would be necessary to achieve this. In a sprawling position the dorsally-facing head comes into contact with the ventrally-facing dorsal margin of the acetabulum. Also, the condyles on the femur for articulation with the tibia and fibula are ventrally-facing, suggesting that the crus was at right angles to the femur, in turn implying that this was perpendicular to the acetabulum.

The muscle configuration of the hind limb (Fig. 7B, F-G) would seem to support this conclusion, since, judging from their areas of attachment, muscles such as the pubo-ischio-femorales externus, ventral adductor, femorotibialis and gastrocnemius were all well developed. The former two muscles would certainly have had a postural function. The latter two, although concerned with flexing the limb, would also have been important posturally.

However, the position of the head on the anteromedial extremity of the femur does suggest in-turning of the bone implicated in the change from a sprawling to a more erect limb position. If the femur of *Robertia* is compared with that of a pelycosaur such as *Dimetrodon*, however, it can be seen that the head of *Robertia* is not so much in-turned but rather that the posteromedial part of the articular surface has been reduced (Fig. 11). Also, the articular surface of the femur of *Robertia* has become more rounded and bulbous and concentrated on the dorsal side. The obvious consequence of these changes in a sprawling-gaited animal would be to allow a longer protraction-retraction arc before the posterior margin of the femur touched the border of the acetabulum and before contact of the femur head and the acetabulum was lost. In particular,

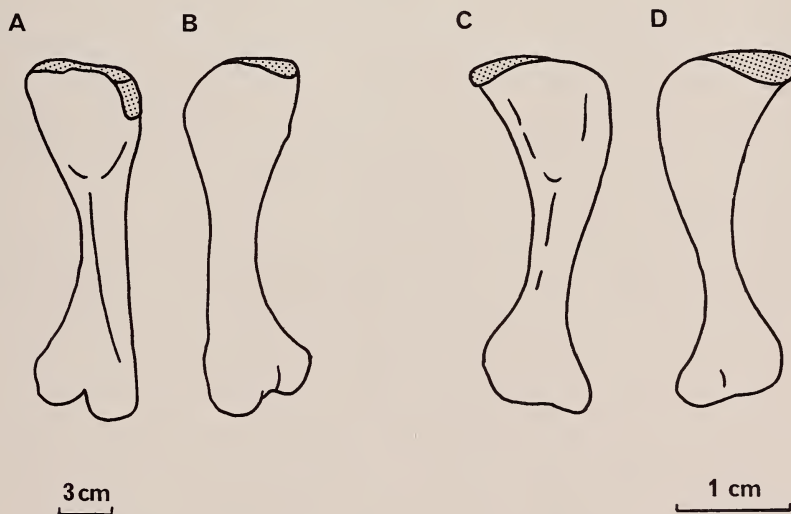


Fig. 11. A comparison of the femora of *Dimetrodon* and *Robertia* reduced to the same approximate length (*Dimetrodon* after Romer 1922). A. *Dimetrodon*, right femur ventral. B. *Dimetrodon*, right femur dorsal. C. *Robertia*, right femur ventral. D. *Robertia*, right femur dorsal. (The articular surface of the proximal end is stippled.)

the positioning of the head on the anterior extremity of the femur allows a great degree of protraction since there is no part of the femur anterior to the head to touch the girdle. Jenkins (1971) notes that in *Dimetrodon* during no part of the stride could the femur be directed more anteriorly than medially because of the shape of the head of the femur. The anterior position of the head in *Robertia* can, therefore, be seen as an adaptation to extensive protraction as a way of lengthening the stride.

However, although retaining a sprawling gait, there is no sign in *Robertia* of a powerful caudifemoralis acting as a retractor. Instead the iliofemoralis must have had this role. With the femur in a sprawling position the iliofemoralis can act as a retractor only if its origin is on the posterior part of the ilium. If its origin is more anterior, then the insertion must be posterior to the point of rotation of the femur in the acetabulum, that is, on a pronounced trochanter major. In *Robertia* there is no such pronounced trochanter major, so even a far anterior origin would not allow the iliofemoralis to act as a retractor, and, in fact, it is seen that the ilium is not expanded far anteriorly, and quite possibly the anterior margin was occupied by the iliotibialis in any case. In *Robertia* probably the farthest anterior that the iliofemoralis fibres insert is over the acetabulum. These fibres would only retract the femur from a midstride position. When the femur was fully protracted, posteriorly-originating fibres would be necessary to initiate retraction. The posterior extension of the ilium was, therefore, necessary to provide adequate origin for this part of the iliofemoralis.

However, this does not explain why the iliofemoralis took over from the caudifemoralis as a retractor muscle. Possibly as the excursion of the femur became greater, especially the point to which it could be protracted, then the fibres of the caudifemoralis might have been too short to allow the increased degree of protraction. This problem does not face the iliofemoralis, since, whether the limb is protracted or retracted, the length between the origin and insertion of the iliofemoralis does not change a great deal because its origin is above the femur rather than far posterior to it.

If the iliofemoralis, by gaining a more posterior insertion on the femur, could function equally well as the caudifemoralis as a retractor, then the further evolution of the iliofemoralis may be favoured for another reason. If the insertion migrated on to the posterior edge of the femur, or better still, on to the ventral margin of the posterior edge, then the muscle could also cause long axis rotation. This would be in an anti-clockwise direction on the left-hand side, forcing the crus backwards. The powerful extensor muscles (femorotibialis) could then extend the limb, imparting a forward thrust to the body. This would be a significant contribution to the overall locomotory thrust developed.

This development of long axis rotation might have been very important since, in later dicynodonts when a larger trochanter major is developed, retraction becomes more limited because the trochanter touches the acetabulum. However, by this time long axis rotation is well established in the limb movement and contributes greatly to the stride.

The above arguments imply that reduction of the length of the tail occurred concomitantly with the reorganization of the iliofemoralis muscle and was a rather passive process: as the iliofemoralis became the main retractor muscle, the caudifemoralis was no longer needed and therefore its origin (the caudal vertebrae) could be reduced. However, an alternative view, that reduction of the tail was actively selected for and that reorganization of the iliofemoralis followed as a consequence of this, is also possible. In this case one would need to postulate a selective pressure for tail-shortening. Geist (1972) suggests that tail-shortening would be favoured in therapsids that lived in cool environments as a means of reducing heat loss. A shorter tail and other appendages would help the animal to approximate to a sphere, giving the most advantageous surface area : volume ratio. Geist argues that having reduced heat loss, such therapsids could maintain a fairly high body temperature without the need to consume vast quantities of food. To be most successful these adaptations would be coupled to large size, and Geist cites *Kannemeyeria* as an example of such a homeotherm.

Geist attempts to demonstrate the change in surface area brought about in a hypothetical animal when the length of its tail is reduced by half, keeping the total mass of the body constant. A similar exercise can be carried out with *Robertia*, first allowing a tail 10 cm long (which is approximately two-thirds body length) and then allowing a tail length of 4 cm (which is the approximate actual length of the tail). The surface area: volume ratios obtained are very approximate since Geist's method reduces the form of the animal to a right regular conical head, a cylindrical body, and a conical tail. The ratios obtained for *Robertia* are, with the long tail 0.775, and with the short (actual) tail 0.665. The change in the ratio is 14.21 per cent. This is obviously a substantial change and would be significant to the animal's temperature control system. However, to achieve this the volume of the tail (presumably mostly muscle) has been reduced by 80 per cent. It is difficult to envisage such a reduction occurring in one evolutionary event since it will have great repercussions on the reptilian mode of locomotion. However, if the reduction occurred gradually, it is difficult to see the advantage in terms of thermoregulation that the incipient stages would bring. In conclusion, then, although tail reduction may benefit an animal by reducing its surface area once a short tail was fully evolved, it is difficult to imagine this as a prime selective pressure.

It is possible, instead, to visualize tail reduction as part of a suite of characters which enable an animal to become more manoeuvrable during locomotion, as discussed in connection with the forelimb. This increased manoeuvrability may not only be advantageous at high speeds, but also at low speeds over uneven terrain. It would then assume great importance for small animals to whom even small discontinuities in the terrain pose large problems of manoeuvrability.

One stage in producing this manoeuvrability would be reduction of lateral undulation in the locomotory pattern. Although *Robertia* still seems to retain

the possibility of lateral flexibility (see page 226), later dicynodonts such as *Dicynodon trigonocephalus* (King 1981) do not. Kemp (1980) has indicated the possible advantages of an animal possessing a rigid vertebral column:

1. During fast locomotion, momentum would be maintained if the animal followed a linear path. Lateral deviation from this path by parts of the body would cause a loss of momentum.

2. If the hind limb produces most of the significant locomotory thrust, then the whole of the locomotory forces applied to the animal pass forward along the spinal column. Any slight distortion of the vertebral column then leads to a large bending moment, tending to cause collapse of the animal between fore and hind limbs.

It has been shown earlier (page 213) that most of the muscles of the pectoral girdle in *Robertia* had a postural function and it is possible, therefore, that the forelimb produced a much weaker locomotory thrust than the hind limb. Both of the advantages listed above might then have applied to *Robertia*. Furthermore, during lateral undulation the head would be moving continually from side to side. This may be a grave disadvantage for an animal feeding on small invertebrates which it may need to catch while running. Both Cruickshank (1980 pers. comm.) and Cluver (1978) have suggested that small dicynodonts might have included terrestrial invertebrates in their diet, and therefore the ability to both sight and catch prey effectively might have been a factor in keeping the path of the head as straight as possible during locomotion.

Manoeuvrable animals sacrifice some stability for agility. Instead of relying on body proportions and size for stability, they tend to rely on postural changes brought about by neuromuscular control to counteract overbalancing forces. If a loose inverse relationship between stability and manoeuvrability is assumed, then it is possible that loss or reduction of a tail may increase manoeuvrability by decreasing stability. The tail could act as a stabilizing organ in the following way: an animal relying on lateral undulation in its locomotory pattern faces a problem of instability; as the animal flexes its body the limb on the convex side of the flexure will be off the ground, in the act of completing the recovery stroke; because of the body flexure the triangle formed by the other three anchored legs may be so placed that there is a possibility of the animal's centre of gravity falling outside the triangle; it would, therefore, tend to collapse in the direction of the unanchored leg; this tendency could be counteracted by a fairly massive tail flexed in the same direction as the head, that is, away from the unanchored leg. Now, if the possibility of lateral undulation is lost, as in the later dicynodonts, then the tail is not needed as a balancing organ. In fact, if increased manoeuvrability is being selected, then a large tail with a large moment of inertia is actually undesirable.

A third stage in increasing manoeuvrability would be to accentuate the problem of instability outlined above by decreasing the triangular area formed by the anchored leg. One way of doing this is by altering the stance of the animal from a sprawling mode to one where the legs are pulled in underneath

the body. At the expense of stability the animal can bank and turn rapidly if necessary.

There is probably no fixed order in which these stages should appear in therapsid evolution. They must to some extent appear together. In *Robertia* lateral undulation has not been eliminated nor are the legs turned in under the body, but the tail is shortened. In later dicynodonts such as *Dicynodon trigonocephalus*, the tail is short, lateral undulation has been reduced and the hind limbs are pulled in somewhat. Such a suite of characters may be widespread in the mammal-like reptiles.

AXIAL SKELETON

Various sequences of vertebrae and ribs are present in the specimens. None is complete from neck to tail, however, so the total number of vertebrae in the column is uncertain. The pre-sacral number is probably approximately twenty-six. Two sacral vertebrae are preserved and eleven caudal.

The atlas and axis vertebrae are damaged but appear to have the same forms as that described in *Dicynodon trigonocephalus* (King 1981). The neck vertebrae following (Fig. 12A) have slightly shorter neural spines than subsequent vertebrae and show the distinctive facets for the double-headed ribs (Fig. 12A: r fa), one on the centrum and the other on the transverse process. Proceeding from vertebra 4 to vertebra 7, it is seen that the centrum facet gradually increases in area and migrates dorsally on the centrum. Gradually the transverse process facet is lost, the sole articulatory facet being the elongate centrum facet as on vertebra 15 (Fig. 12B). The point at which the two heads of the rib coalesce is not known in this case. It is usually about vertebra 9 or 10. As in other dicynodont specimens, the ribs of vertebra 8 and 9 are particularly robust and bear a pronounced fossa on the midline of the posterior surface (Fig. 13D: p fo). The fossa between the two heads on the posterior surface is also very pronounced (Fig. 13D: h fo).

In the posterior dorsal vertebrae the rib facet begins to decrease in area, and migrates upwards towards the transverse process (Fig. 12C: r fa). The ribs associated with these vertebrae are also much less robust. After the particularly robust ribs of the shoulder region, there is a trend towards lighter but long ribs in the dorsal region (Fig. 13E). However, these begin to decrease in length at about vertebra 21 and are much reduced by vertebra 26 (Fig. 13F).

Several of the mid-dorsal and thoracic ribs are complete, though broken. Viewed posteriorly or anteriorly, the rib is a smooth arc of a circle of very long radius. There is no sudden change in the radius of curvature. Viewed dorsally, the ribs have a distinct backward as well as downward curvature. Because the ribs of the thoracic and lumbar regions of the spinal column are so long (almost twice the length of the epipodial) and rather straight, they must have been orientated backward in the body at a considerable angle (Fig. 15). Even so, the thorax and abdomen were probably only just clear of the ground in the normal stance. The cross-section of the thorax would have been almost circular.

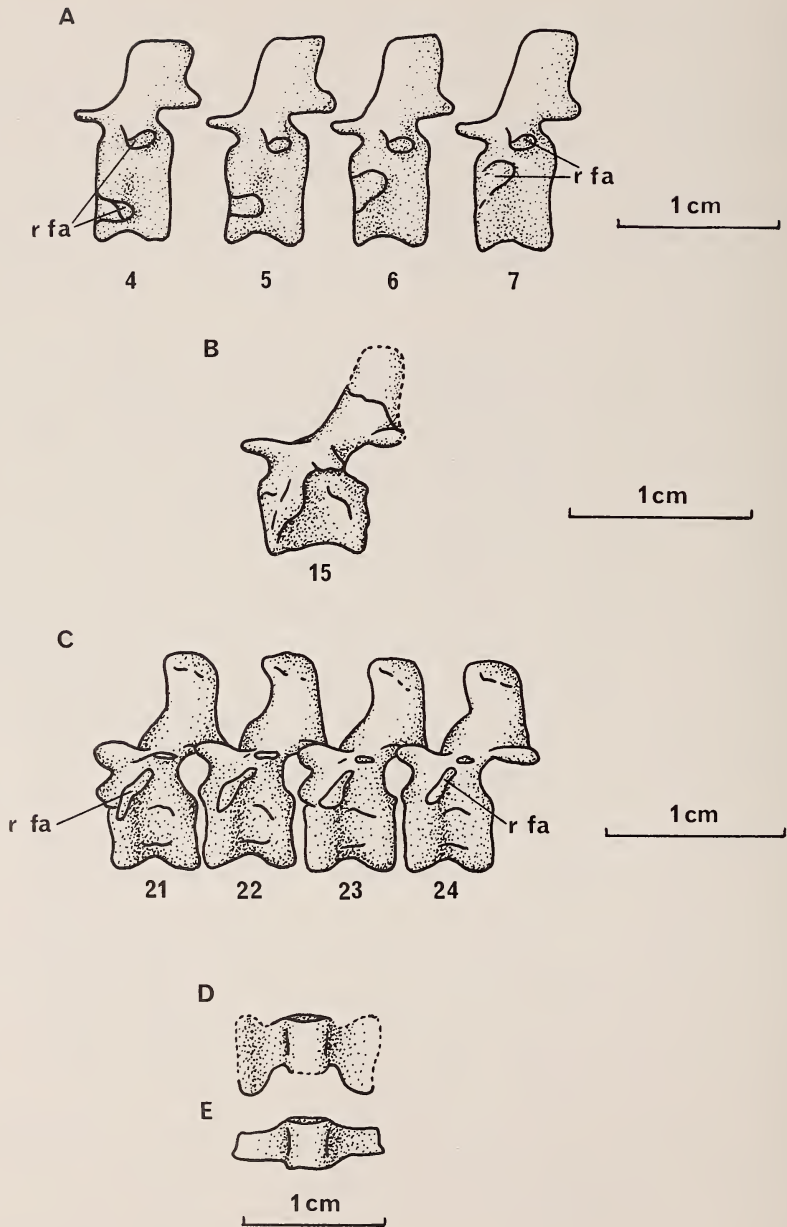


Fig. 12. *Robertia broomiana*, vertebrae. A. Vertebrae 4 to 7 lateral. B. Vertebra 15 lateral. C. Vertebrae 21 to 24 lateral. D. Second? sacral vertebra ventral. E. Third? sacral vertebra ventral. (A reconstructed from cast 5; B reconstructed from cast 6; C reconstructed from cast 8; D-E reconstructed from cast 7.)

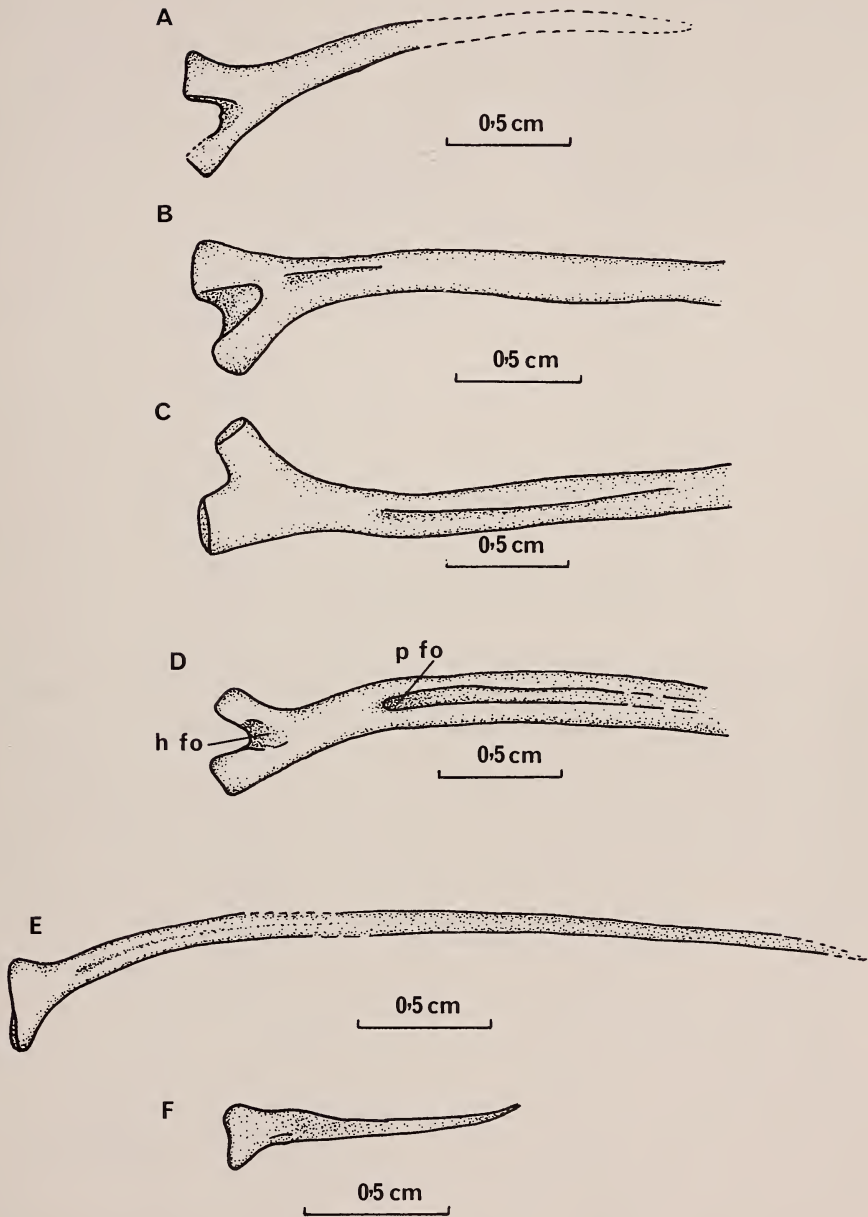


Fig. 13. *Robertia broomiana*, ribs. A. Rib 2 or 3 posterior. B. Rib (probably 6) posterior. C. Rib (probably 6) anterior. D. Rib (probably 8) posterior. E. Mid-dorsal rib anterior. F. Last presacral rib anterior. (A-C reconstructed from cast 5; D reconstructed from cast 3; E reconstructed from cast 6; F reconstructed from cast 8.)

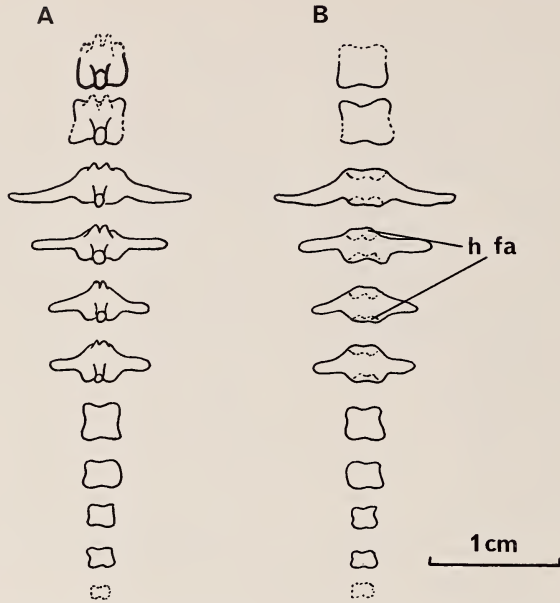


Fig. 14. *Robertia broomiana*, caudal vertebrae. A. Dorsal. B. Ventral. (Reconstructed from casts 7 and 9.)

The zygapophyses of the pre-sacral vertebrae do not show much morphological change along the column. The anterior zygapophyses tend to be shallow and wide, forming articulations with the posterior zygapophyses which are almost horizontal. Presumably these allowed extensive side-to-side movements of the vertebrae, so that in a horizontal plane the vertebral column was very flexible. This flexibility and the long, slender body must have made *Robertia* appear quite lizard-like. The limb proportions of a small lizard such as *Lacerta ocellata* are also similar to *Robertia*'s including the slightly longer dimensions of the hind limb compared to the forelimb. Unlike *Lacerta*, however, the forelimb of *Robertia* is very robust.

The neural spines of the pre-sacral vertebrae do not slope backward to any great degree and are quite short, being less than the height of the centrum.

Two sacral vertebrae are preserved but presumably more were present in life (Fig. 12D-E). It does not seem likely that more than three were present in life though, judging from the length of the ilium and the length of the sacral ribs. Of the two vertebrae preserved, the ribs are much more expanded on the anterior, and it is possible that they represent the second and third sacral vertebrae, respectively.

The tail is reasonably well preserved (Fig. 14). The first two caudal vertebrae have no ribs attached to them. The next four vertebrae have fused ribs which gradually diminish in size along the column. Traces of haemal arch facets (Fig. 14B: h fa) can be seen on these vertebrae. The last five vertebrae are

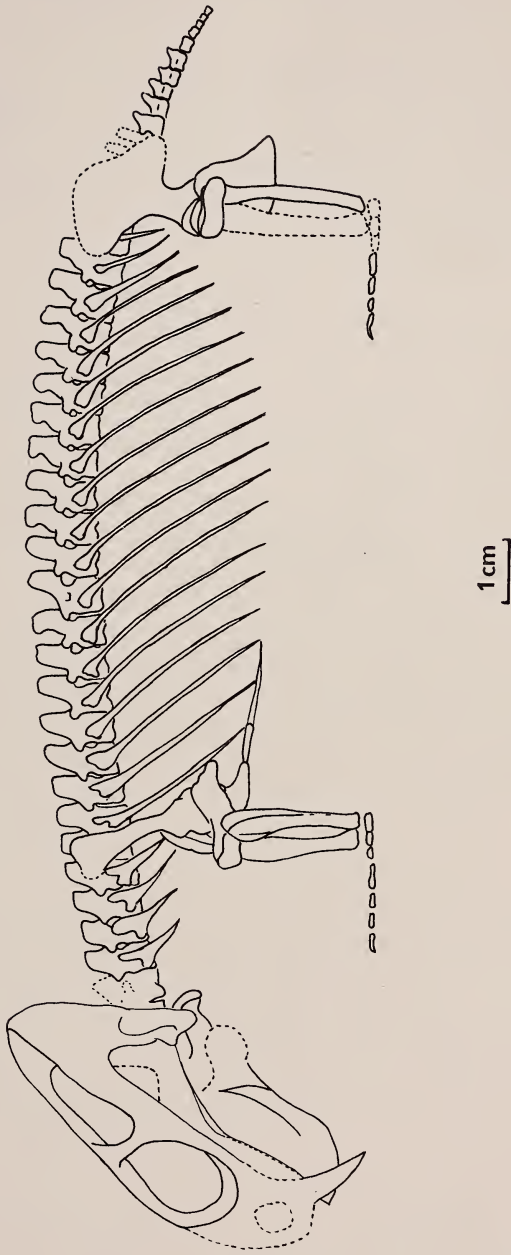


Fig. 15. *Robertia broomiana*, a reconstruction of the entire skeleton.

cuboids of bone with few distinguishing features preserved. The tail is thus short, approximately one-eighth body length, and, judging from the limited area for muscle attachment, also lightly built.

SUMMARY AND CONCLUSIONS

The postcranial skeleton of *Robertia broomiana* shows a mixture of advanced and primitive characters which may be expected of an early (*Tapinocephalus* zone) dicynodont. The specialized characters of dicynodonts include the production and eversion of the acromion process; the reduction of the pre-glenoid area of the scapula; the medial origin of the supracoracoideus muscle; the posterior and anterior extension of the ilium; the reduced caudifemoralis muscle and the role of the iliofemoralis as the limb retractor; reduction of the fourth trochanter; absence of an internal trochanter; anterior position of the head of the femur; the short tail; the large thorax and abdomen; and the digital formula. Many of these characters are as fully developed in *Robertia* as they are in much later dicynodonts. The lack of elaboration of the iliofemoralis is an exception to this.

Features of *Robertia* which appear to be primitive for therapsids generally include the sprawling position of the forelimb; extensive postural musculature and musculature associated with forelimb extension; the remnant of an ectepicondylar foramen; the small trochanter major; the small extension of the anterior edge of the ilium; large hind limb postural muscles; the small number of sacral ribs; the sprawling position of the femur; the flexible spine.

Robertia was a small, probably rather active animal, a little like modern lizards. Although an analysis of the skull is necessary before any conclusions can be drawn, it is not impossible that *Robertia* not only fed on softer plant matter but also on small invertebrates, when the teeth may have played a part in food capture or processing

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ABBREVIATIONS

| | |
|-------|--------------------------------|
| ac | acetabulum |
| ac p | acromion process |
| add | adductor muscles |
| b | boss |
| br | brachialis muscles |
| cb | coracobrachialis muscle |
| cb l | coracobrachialis longus muscle |
| ce? | possible centrale |
| c fa | coracoid facet of the glenoid |
| cl | clavicle |
| cor | coracoid |
| d | dentary |
| d e | distal end of the clavicle |
| del | deltoid muscle |
| d fo | deep fossa |
| d p c | deltopectoral crest |
| d s | dentary shelf |
| ect f | extepicondylar foramen |
| e fo | elongate fossa |
| ent f | entepicondylar foramen |
| fo | fossa |
| f r | flat ridge |
| ft | femorotibialis muscle |

| | |
|---------|---|
| gas | gastrocnemius muscle |
| gl fa | scapula facet of the glenoid |
| h | hollowing out of the ilium |
| hd | head |
| h fa | haemal arch facet |
| h fo | fossa between the heads of a rib |
| ic | interclavicle |
| if | iliofemoralis muscle |
| il | ilium |
| int | intermedium |
| is | ischium |
| i-t | origin of the ischiotrochantericus muscle |
| la fo | fossa on the lateral surface of the ilium |
| l d | attachment of the latissimus dorsi muscle |
| l r | low ridge |
| m fo | marked fossa |
| m r | medial ridge |
| mx | maxilla |
| n | notch |
| o fo | oval fossa |
| o p | olecranon process |
| p | parietal |
| pal | palatine |
| pc | precoracoid |
| pec | pectoralis muscles |
| p fo | fossa on the posterior surface of a rib |
| pi | pisiform |
| p i f e | pubo-ischio-femoralis externus muscle |
| p i f i | pubo-ischio-femoralis internus muscle |
| pmx | premaxilla |
| pof | postfrontal |
| pp | preparietal |
| pr fo | proximal fossa |
| pro | protuberance |
| pt | pterygoid |
| pu | pubis |
| q | quadrate |
| rad | radius |
| r | ridge |
| ra | radiale |
| r a | rugose area |
| rad fa | radial facet on the humerus |
| r fa | rib facet |
| r fo | rugose fossa |
| sbsc | subscapularis muscle |
| sca | scapula |
| sc | supracoracoideus muscle |
| s fo | shallow fossa |
| s h | scapulohumeralis muscle |
| sm sw | small swelling |
| sq | squamosal |
| s r | short ridge |
| str | striations |
| sw | swelling |
| t | teeth |
| t fo | triangular fossa |
| t h l | triceps humeralis lateralis muscle |
| t h m | triceps humeralis medialis muscle |
| t m | trochanter major |

| | |
|-------|--|
| tr | trough |
| tub | tubercle |
| u | ulna |
| ul fa | ulnar facet on the humerus |
| v | vertebra |
| v s | ventral surface of the deltopectoral crest |
| I-V | digit numbers |